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Current Genetic Thought and Dairy Cattle Breeding

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SINCE the rediscovery of Mendel's laws of inheritance in the early years of this century, the ideas about their practical application to animal breeding have changed continually. The direction these changes took depended in the final analysis on the current theory of the mode of inheritance of the economically important characters involved. In the beginning, quite an effort was spent in attempting to explain differences in milk production on the basis of a few genes with major effects. Later, when it became generally accepted that these characteristics depended on a large number of genes whose individual effects could not be detected (polygenic inheritance), the controversy centred around the question whether the genes involved were mainly additive in their action or whether interacting genes played a major role in causing inherited differences between individuals. This question is still largely unsolved and is causing the present controversy between the proponents of selective breeding on the one hand and cross-breeding on the other. In the last two decades a new science, known variously as Population Genetics (8) or Biometrical Genetics (11) has grown up to explore and explain the consequences of polygenic inheritance.

The general acceptance amongst geneticists of the theory of polygenic inheritance in regard to quantitative characters has not brought about any spectacular change in pratical animal breeding. The reasons for this are fairly clear: to a farmer the theory is unattractive; it is difficult to understand, as it abstractly deals with populations rather than with individuals—it promises probable results rather than near-certainties. Finally, as on the theory's own premises progress must necessarily be slow, it cannot win immediate popularity. Farmers naturally like to see some results of their work during their lifetime. Herd improvement based on the theory of polygenic inheritance thus requires a highly educated farming population, and in addition nation-wide organisations for collecting and interpreting production results. As these premises are fulfilled to a considerable extent at the present time in New Zealand, it seems appropriate to examine critically the present state of knowledge in order to place the future of dairy cattle improvement on the soundest possible basis. This is the more important now, when technically solved artificial insemination provides the animal breeder with a new powerful aid, but at the same time brings with it a number of problems which may have dangerous consequences if not handled correctly.

The simplest method to convey the current genetic theories as applied to animal breeding is perhaps to discuss them in relation to the two most important systems of mating: inbreeding and outbreeding, and finally consider some aspects of selection.

1. Inbreeding implies the mating of individuals which are more closely related to each other than to the rest of the population to which they belong. The main feature of inbreeding is that it has the power to fix allelic genes and thus fix desirable characters to the extent these are under hereditary control. This system of breeding has long been favoured by both breeders and scientists and especially the variant described as line breeding still holds many a breeder spellbound. However, this attitude is beginning to change, and it is now generally conceded that inbreeding, except in a very mild form, has in practice detrimental effects on most characters of economic importance. This

happens because a number of recessive genes with a lowering effect on general vigour in the course of inbreeding become homozygous and can thus assert their influence. It seems that in dairy cattle an inbreeding co-efficient of 10% (or rather less than is achieved by one generation of half-brother-half-sister mating) is the safety limit (see (14) for references). In spite of this, there is a definite place for inbreeding but only in conjunction with other systems of mating. As it is the only efficient method of uncovering undesirable recessives, inbreeding may have to be used, for instance, in a selection programme involving the use of A.I. Also, if hybrid vigour is an important factor in high production, it may be necessary to produce inbred lines as a prerequisite to outcrossing. This point will be discussed further presently. Meanwhile, it is perhaps appropriate to point out some commonly held misapprehensions in regard to the effects of inbreeding.

One of the alleged advantages of inbred stock is the theoretically smaller variability shown between individuals of the herd. Actually, two opposing trends occur: within inbred lines the genetic variation decreases, but increases between the lines. Depending on the number of inbred lines kept going, this may result in a net increase in the total genetic variation of the herd. If, on the other hand, all but one inbred line are discarded, the amount of genetic variation, and hence the possibility of further gain, will soon be exhausted. While it is thus possible to reduce drastically the genetic variability through inbreeding, the total variation will not show a commensurable decrease. This is due to the fact that the greatest part of the total variation (75% or more in most economic traits) is of non-genetic origin. For instance, in stock inbred to such an extent that the genetic variability is reduced by 25%, the total variability is only decreased by 6% or less. Further, there are good reasons to believe that the reduction of total variability in practice will be even smaller than this, in that inbred stock, by virtue of the great number of homozygous recessive genes they carry, are somatically badly balanced and are therefore more sensitive to small environmental changes than non-inbred stock.

Outbreeding and cross-breeding involve mating of individuals which are not more closely related to each other than to the average of the population. Outbreeding generally denotes a system in which inbred lines are crossed, while in cross-breeding animals of different breeds are mated together. Both types of mating are used in order to take advantage of what is commonly known as hybrid vigour of heterosis. The gene mechanism responsible for hybrid vigour is not fully known, but it seems likely that many different kinds of gene interactions are involved. According to the oldest theory, heterosis is due to an accumulation of dominant genes (7), but it is nowadays generally thought that this theory, on its own, cannot explain the whole observed effect (3). Two other mechanisms that may be invoked are overdominance and epistasis. According to the first hypothesis, hybrid vigour manifests itself as a result of the heterozygote being more vigorous than either homozygotes or, in other words, the individual who carries the gene pair Aa has the advantage over individuals with either AA or aa. If epistasis is important, it would mean that a character reaches fullest expression only if, say, a gene A on one chromosome is accompanied by the genes c, D, e on other chromosomes. Quite different breeding programmes would be required, depending on which view was taken regarding the basis of hybrid vigour. If the dominance theory is accepted, the most efficient programme would be to inbreed a number of separate lines and subsequently test cross these until the two lines producing the best hybrid offspring were found. To utilise the effect of overdominance and epistasis it is necessary to select two strains or breeds and test cross the males of one strain against the females of the other, and vice versa. The best animals (on the basis of this progeny test) are kept to reproduce the lines. A preliminary inbreeding of the lines does not seem necessary. This scheme has been named rather grandiosely "recurrent reciprocal selection for special combinability," but is really the same thing as "selection of strains for nicking"—an effect that many dairy men believe to occur, although the evidence is almost non-existent.

The great success attained by maize breeders in the utilisation of hybrid vigour has, however, given a strong impetus to similar attempts among animal breeders, and at the present time most of the efforts spent by research workers on animal breeding problems are in this direction. Their primary task is naturally to show that hybrid vigour is an important factor in milk production. If this is proved, it still remains to be demonstrated how such a finding can be translated into practice. It can be noted that, if dominance is the most important factor, it would be difficult to utilise heterosis in dairy cattle breeding since the development and maintenance of a large number of highly inbred lines would be a very difficult and expensive task, while on the other hand a mechanism depending on overdominance or epistasis would not present the breeder with nearly the same amount of difficulties.

The whole concept of heterosis rests on the assumption that there exists a residual gene effect after the additive genetic variation has been accounted for. For this the evidence is not clear cut, although the use of identical twins in experimental work promises to provide a definite answer. But before discussing this point it is necessary to introduce the idea of heritability.

One of the fundamental corollaries of polygenic inheritance is that characters inherited this way are easily influenced by environmental factors, or in other words they are of low heritability or are "poorly inherited." The heritability coefficient is a measure of the fraction of the total variation which depends on inheritance. Thus, when it is stated that butterfat production is inherited to the extent of 25%, this means that of the total observed variation amongst the individuals of a herd 25% can be accounted for by differences in their genetic make-up. As generally quoted, the figure includes only the part of the genetic variation which is inherited through additive genes ,or in other words the portion of the total genetic variation which can be passed on from parent to offspring, while dominance and other effects caused by gene interaction are excluded. The remaining variation is due to differences in environment (permanent or temporary) which is not common to all individuals within the herd. There are a great variety of factors of this type: pre-natal environment, diseases, differences in calving times, inter-seasonal fluctuations in nutrition, and so on. This part also contains the differences in production due to errors in the measurement and calculation of yields.

The heritability coefficient can be estimated from the relative similarity shown by closely related animals. Dam-daughter and half-sister comparisons are the most commonly used in the calculation of the coefficients for milk and butterfat yield. These have been found to be low or, as already mentioned, of the order of 25% (6). This method of computation does not allow the partitioning of the remaining 75% into its component parts. The environmental fraction includes, therefore, in addition to all true environmental effects, also some purely genetic variation due to dominance and other gene interactions and also the interactions between environment and genotype.

Using identical twins, a heritability value can be found which also includes the non-additive gene effects. The Ruakura work on twins indicates that this value is astonishingly high, or approximately 80%, when derived from split-twin experiments, and even higher, 90% or more, when derived from uniformity trials. The question inevitably arises whether all of the difference between a heritability of 80% from twin experiments and 25% according to the orthodox method can be ascribed to non-additive gene effect. The answer is definitely: No. In the work on twins the environment was under much stricter control than under ordinary farm conditions and there was practically no variation due to imperfect measurement of the yields. Indeed, the Danish Progeny Test Station results show that the additive genetic fraction is of the order of 70% when computed from records of groups of half-sisters which have been managed under conditions as strictly controlled as in the twin experiments. It therefore appears that the non-additive fraction cannot amount to more than 15-20% of the total genetic variation. This is thus the margin on which the hopes of utilization of hybrid vigour must be based. It may seem slender, but may still be of importance, especially when additive genetic variation has been much reduced as a result of selection. A system of cross-breeding would actually fit very well into the New Zealand dairy farming picture, especially if it is granted that a greater stratification of the industry is desirable. It seems rather an economic waste to rear dairy stock on first-class land when this could be done much more cheaply on second-class land, and there is, in actual fact, already quite a migration of dairy heifers from the hills of Taranaki to the milking pastures of Waikato. Many of these heifers are cross-bred (generally Ayrshire x Jersey) and there are many farmers who prefer stock showing "plenty of colour." It is thus a breeding system that would not seem too outlandish to some New Zealand dairy farmers. This is quite an important advantage from the operational point of view.

The national dairy cattle breeding policy in New Zealand is, however, geared to a selection programme involving neither inbreeding nor outbreeding. It is therefore of greatest importance to consider the main factors influencing the rate of progress which may be obtained through selection, its limitations and possible dangers.

Progress in selection depends on three factors: (1) Intensity; (2) Accuracy; and (3) Generation turnover.

The intensity of selection is measured by the average genetic superiority of the animals saved for reproduction over the rest of the herd. Thus, the selection intensity reaches a maximum value when the number of animals required for reproduction is reduced to a minimum.

It has long been shown that in practice the intensity of selection on the cow side is so low that very little progress can be made through selection on the female side. The rest of this discussion will therefore be confined to the selection of bulls.

The advantage of Artificial Insemination is based on the fact that the intensity of selection of bulls can be increased manyfold, in that only a few of the very best bulls are required for reproduction. But if A.I. is to have the desired effect, it is necessary that the bulls used are of the very highest genetic quality, or in other words the outcome depends on the accuracy with which the bulls are selected. The average production of a number of his daughters is the most precise test yet devised to ascertain a bull's inherited capacity. This is commonly known as the progeny test. In general, there are two conditions which make the precise assessment of the progeny test difficult: (1) milk and butterfat production levels are governed to a great extent by other than inherited factors, and (2) the sampling nature of the test introduces errors. Thus the precision of the test increases when differences in environment between and within progeny groups are as small as possible. It increases also with increase in number of daughters. However, fewer bulls can be tested as the number of daughters required for test increases, which results in a reduction of the selection intensity. It is obvious that a balance must be struck between the number of bulls to be tested and the number of daughters required in each progeny group. These aspects of sire survey seem of such importance that they warrant a detailed discussion.

There are three main methods of testing bulls. In order of decreasing accuracy (assuming the same number of daughters to each bull) they are:—

(1) In the **Progeny test station scheme,** the daughter groups of all bulls selected for comparison are assembled at a special station where they are subjected to a strictly uniform and strictly controlled environment. This method is used in Denmark.

(2) In the **Sire Survey scheme,** bulls are compared on the basis of their daughters' records achieved under ordinary farming conditions. In general, all daughters of each bull are tested in one herd. The progeny groups are subjected to widely different environment, depending on the feeding and care of the owner farmer, but there are relatively small differences within the groups. This is the method used at the present time in New Zealand.

(3) In the **A.I. scheme,** the daughters of each bull are evenly dispersed over a whole range of environments. On the average, all progeny groups are thus subjected to the same environment. Schemes of this type have begun in Great Britain and New Zealand.

The advantages and disadvantages of the schemes are shown in Table I.

From a theoretical point of view, the main differences between the three schemes lie in the relative accuracy with which the genotypic value of the bulls can be assessed. Assuming that 5 daughter records are required per bull under the progeny test station scheme in order to obtain a desired accuracy, some 20 records would be necessary under the Sire Survey scheme and probably more than 50 under the A.I. scheme (5). It was previously stressed, however, that an increase in the number of daughters required to test a bull must cause a reduction in the total number of bulls available for comparison. This in turn causes an inevitable fall in the selection intensity.

From a practical point of view other considerations must be taken into account. While the Progeny Test Station scheme has a decided advantage on grounds of maximum accuracy, it is expensive and for its success demands a farming population which by upbringing is conditioned to a co-operative breeding programme. Even the Danes do not envisage the testing of more than 50 bulls a year under this scheme. For these reasons it is not likely that this scheme will be used in New Zealand for some time to come.

The other two systems are being used in New Zealand and it is therefore important to compare their respective merits. The great disadvantage of the A.I. scheme is that it requires so many daughters to each progeny group that far too few bulls can be tested. On the other hand, most of the advantages (see Table I) are likely to be relatively unimportant. One of the theoretical advantages of the A.I. scheme is that it is possible to subject samples of the daughters of the bulls under test to widely varying environmental conditions, and thus examine the possible importance of genotype-environment interactions. In other words, it is possible to discover those bulls whose daughters are specially adapted for instance to very poor or to very good environments. However, the work on identical twins at Ruakura indicates that interactions of this kind probably are not very important, except in the case of stock with inherited gross abnormalities, such as "undershot jaw" (4).

The very real practical difficulties involved in this scheme makes it probable that bull testing in New Zealand will continue to be based on the Sire Survey scheme. Therefore, it is desirable to examine this scheme critically to find its limitations and, if possible, to see whether it can be improved upon.

Under the Sire Survey system of New Zealand Dairy Board (15) bulls are compared on the basis of the average production of at least 10 daughters. These are almost always tested in one herd. As there are great differences in feeding and management between the herds, it is obvious that the progeny groups of the various bulls are subjected to large differences in environment. The uncorrected daughter averages are therefore a poor guide to the relative genetic value of the bulls under test.

In general, there is a tendency amongst breeders to underestimate the environmental effects. The experimental work at Ruakura with identical twins indicates that it would be quite possible to explain the whole range of daughter averages obtained in the Sire Survey scheme in terms of differences in herd environments. There is thus no a priori evidence that a bull who leaves daughters with an average of, say, 200lb. butterfat in one herd is any worse than a bull with a daughter average of 400lb. in another herd. This situation was soon appreciated by the N.Z. Dairy Board and the value of a sire is now assessed by a comparison of the daughter averages with the average production of the mature cows in the same herd and season.

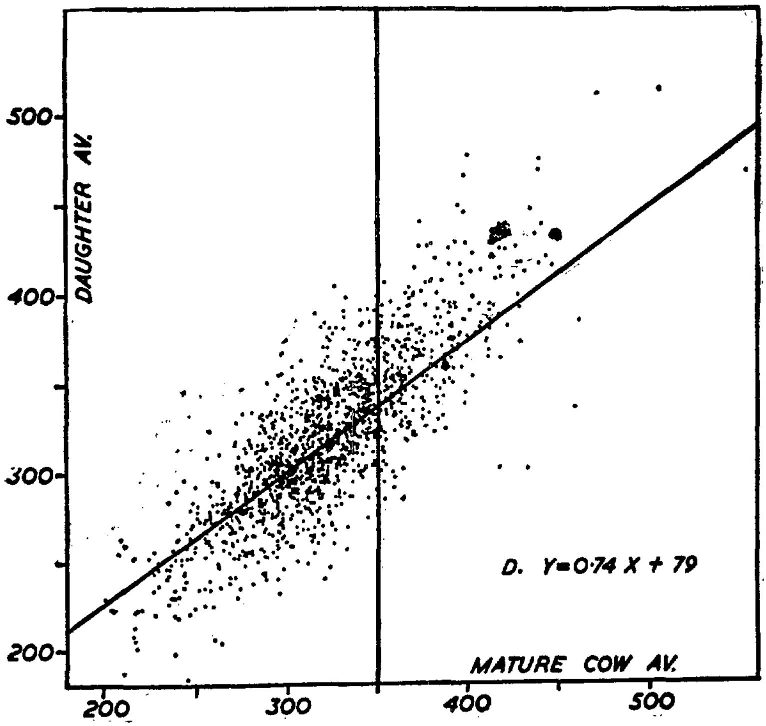

FIGURE 1.

The N.Z. Dairy Board's "Expectancy line" fitted to the data discussed in the text. The vertical line has been drawn in to indicate the fact that more than half of all bulls standing in herds with a mature cow average of 350 lb. butterfat or over qualify as "Merit" Sires.

A complication is added to this method by the empirical finding that in general the bulls used in the lower range of herds leave daughters with higher average production (maturity equivalent) than the mature cows in the same herds. The reverse is true in the higher producing herds. In order to place the comparison of bulls used in herds of different production levels on the same basis, it is therefore necessary to apply a correction. This is made by comparing a bull's daughter average with the expected average production of the daughters of all bulls surveyed in herds of the level in which he was used. Technically this is done with the aid of a regression line (the "expectancy" line) derived from sire survey data. In Fig. 1 the progeny group averages of all sire surveys published in the 7th Edition of the N.Z. Dairy Board Sire Survey and Merit Register were plotted against the mature cow averages and the "expectancy" line drawn in. As it appeared that this line did not fit the present data very well, a regression line was fitted by the least square method. To show how this new line differs from the Dairy Board's expectancy line they are shown together in Fig. 2. It is obvious that according to the new line the daughter averages on the higher levels of herd production do not differ from the mature cow averages to the extent indicated by the Dairy Board's "expectancy" line.

The question naturally arises: Why in any case do bulls used in the lower range leave daughters which in general produce more than the mature cow average while, on the other hand, daughters of bulls used in the higher range are poorer than the mature cows, when

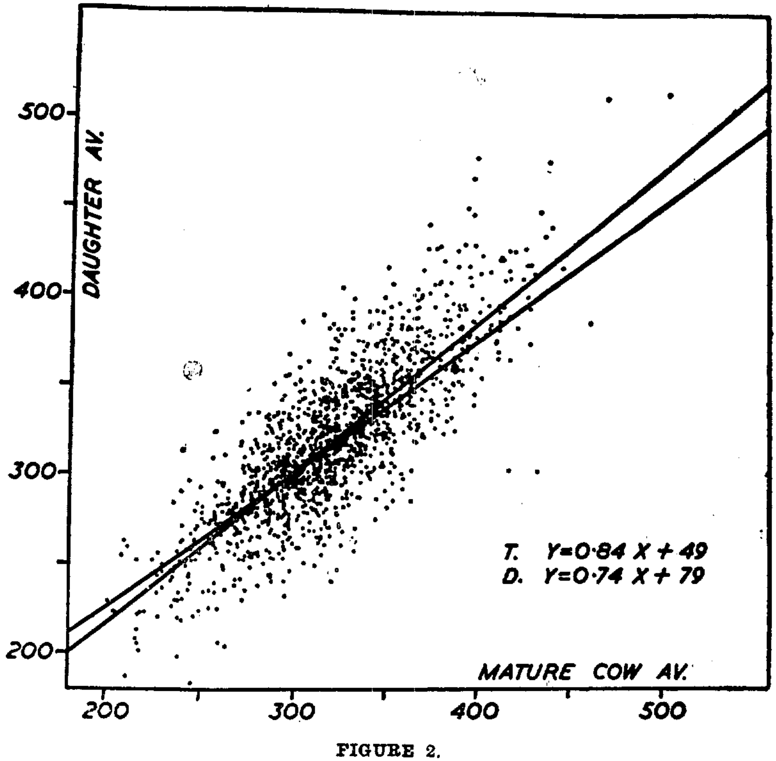

FIGURE 2.

A comparison of the N.Z .Dairy Board's "expectancy line" (top) and a regression line (bottom) fitted by the method of least squares to the data discussed in the text.

logically there should be no such difference? The key to this puzzling feature lies in the fact that the figures of the daughters on which the surveys are based do not represent their actual productions but are mostly maturity corrected records of two and three year olds. It is suggested that the age correction factors do not hold for cows on all levels of herd production. Or in other words: on the lower levels the mature cows produce less than 70lb. above their records as two year olds, while on higher levels they produce more than this amount. The evidence for this can be obtained by the computation of separate regressions for Preliminary and Final Surveys. As the preliminary surveys are based on records all of which are age corrected, while the final surveys comprise at least a proportion of mature records, it follows that the differences between progeny group and mature cow averages should be smaller in the case of the Final Survey than in the Preliminary. That this is so can be seen in Fig. 3, which shows that when more mature records are included in the progeny groups averages (Final Surveys) the slope of the "expectancy" line approaches untiy. (Regression analyses are shown in the Appendix). This question has been discussed in some detail, partly to dispute the commonly held opinion that the average bull used in high producing herds is not able to maintain the production level of these selfsame herds.

The difference between the "expectancy" lines derived from preliminary and final surveys is statistically significant and is of a real practical interest. It seems that it is necessary to use different "expectancy" lines, depending on whether it is attempted to assess a Sire's value on a preliminary or final survey. If a common line is

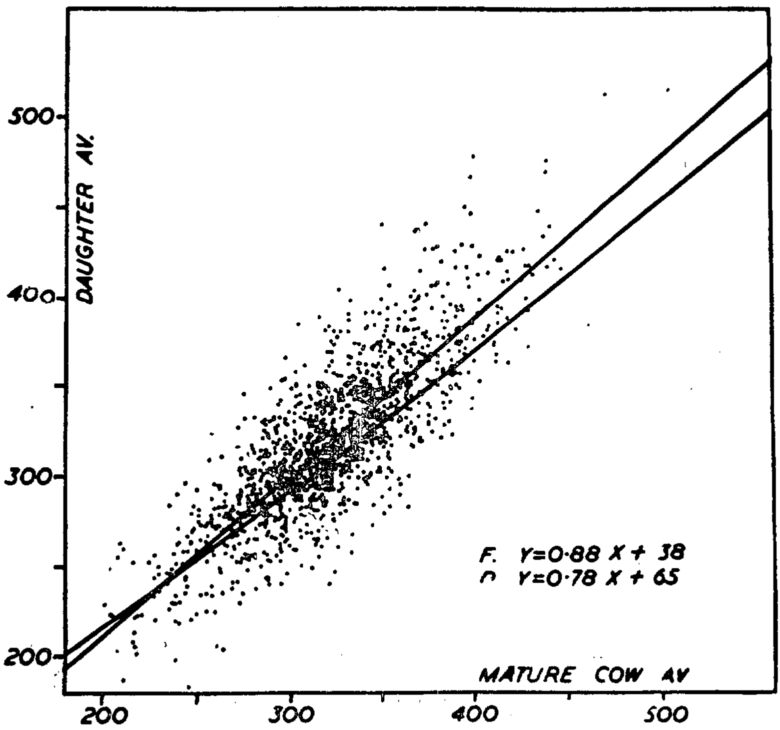

FIGURE 3.
A comparison of the regression line obtained from Final (top) and Preliminary (bottom) Surveys.

used, the bulls with final surveys will be overestimated and those with preliminary surveys underestimated.

Another point worth mentioning is that there is a greater variation amongst the assessed values of sires with preliminary surveys than amongst those with final surveys. (The standard errors of the regression lines are plus or minus 29lb. and plus or minus 23lb. respectively). This is no doubt mainly due to the fact that the preliminary surveys are based on many fewer daughters per sire than the final ones. A greater proportion of the variation in the case of preliminary surveys is thus due to sampling errors than in the case of the final surveys. This situation is also reflected in the fact that, in the case of bulls with final surveys, 74% of the total variation in the daughter averages can be accounted for by the variation in the mature cow productions, while on preliminary surveys the figure is only 61%.

All the above considerations lead to a suggested alteration in the present method of selecting the sires which are most likely to be of superior transmitting ability. According to the method used by the N.Z. Dairy Board, a bull is labelled "Merit Sire" providing his daughters' average production (on the Final Survey) is 350lb. of butterfat or over and are above expectancy. There is also a provision which admits a few bulls with progeny group average below 350lb. into the "Merit" class. In view of the fact that the daughters averages in absolute terms are mainly determined by the production level of the rest of the herd and only to a minor degree by the genetic quality of their sire, it seems that through this procedure the distinction of "Merit Sire" is conferred on a great number of mediocre bulls, while on the other hand many bulls with better transmitting ability are excluded.

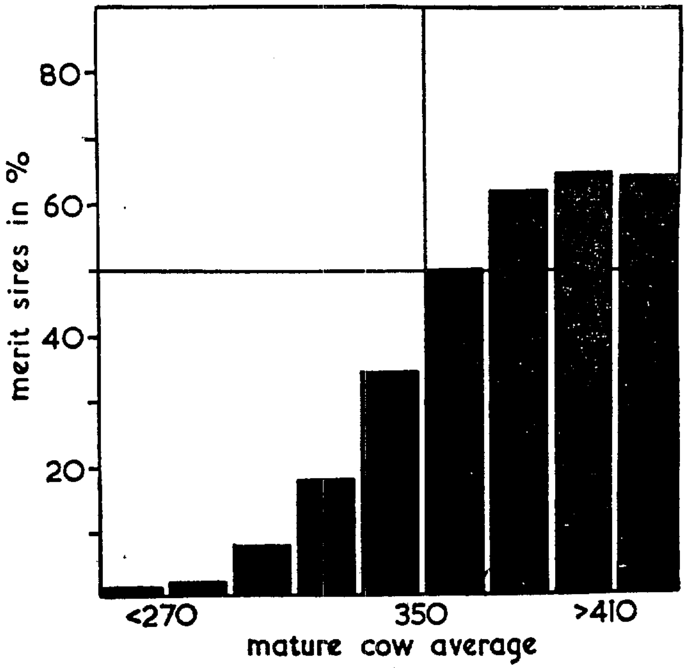

FIGURE 4.

Histogram showing the proportion of bulls qualifying as "Merit" Sires when classified according to the average mature cow production of the herds in which they had been working.

Bulls which have been fortunate enough to be placed in well-fed herds have far greater chances of becoming ''Merit Sires'' than those in poorly-fed herds. 45% of the sires surveyed in above-average herds reach ''Merit' 'standard, while only 8% surveyed in herds below average do so. This is well illustrated in Fig. 4, where the percentages of sires reaching the ''Merit'' standard of daughter production are shown in relation to mature cow averages. The Bulls surveyed in herds with a mature cow average of 350lb. butterfat or above are specially favoured in that no less than 57% of their number reach ''Merit'' standard. The fact that more than half of these bulls are above expectancy demonstrates, incidentally, the poor fit of the Dairy Board's ''expectancy'' line to these data.

To avoid bias of this kind, a better method of selecting bulls for special distinction would be firstly to assess the sire's value in relation to the appropriate ''expectancy'' line (preliminary, intermediate or final, as the case may be be; see Appendix) and secondly to confer distinction on those bulls which exceed the ''expectancy'' by a certain amount of butterfat. This should vary according to the stage of survey: in such a way that a greater excess is required of bulls with preliminary surveys than those with final surveys. It is suggested that the standard errors of the respective ''expectancy'' lines should be taken as the minimum requirements. Under this scheme a bull would become a ''Merit'' sire, irrespective of his daughters' actual production, providing the average of all his daughters' production exceeds the expectancy by 23 or 29lb. of butterfat, depending on the stage of survey. Approximately one-sixth of all surveyed bulls would be expected to make this grade. As a bull's genetic value is known with greater accuracy with an increasing number of daughters in the progeny group, a further refinement of this method would be to base the amount of butterfat required in excess of expectancy on the number of lactations rather than simply on the stage of survey. The minimum standard for bulls selected to be used by A.I. in pedigree herds should preferably be twice as high as for ordinary ''Merit'' sires.

There is an urgent need for research into the question of whether bulls which have proved to be herd improvers in herds of low production standard could be used with the same result in herds of high level of production.

The present Dairy Board recommendation (15) that young bulls should be selected from dams with a high lifetime production seems worth while, when it is considered that a cow's transmitting ability can be measured by the average of five lactations with the same accuracy as a bull's when his progeny test is based on 20 daughters. However, as in the case of ''Merit sires, it seems that in giving the distinction of ''Merit cow the influence of environment must be taken into account, or, in other words, the standard should be flexible and related to the level of herd production.

The knowledge of polygenic inheritance has now advanced to a stage where it is possible to design a breeding programme based on selection which leads to the greatest rate of progress (12). The optimu mstructure depends on the proper balance of a number of factors, of which the following are most important:—

(1) The number of young bulls tested annually;
(2) The number of daughters required in each progeny group.

The previous discussion has covered these two points in some detail. It remains to consider briefly:—

(3) The method of selection of young bulls for testing;
(4) The age at which bulls are tested; and
(5) The size of the breeding unit.

An important factor contributing to an increased rate of progress is the selection of young bulls for testing on the basis of their sire's progeny test and their dam's lifetime production. In practice, it is thus essential that the best progeny-tested sires are used in pedigree herds to provide young bulls for testing.

The age at which the bulls are tested affects the length of generation at intervals and hence the genetic progress per year. Bulls should therefore be test-mated at the youngest possible age.

The optimum size of the breeding unit depends mainly on the fullest possible use of the best proven sires.

As an instance of the maximum rate of progress that can be made when all these factors are taken into account, Robertson and Rendel (12) suggest the following scheme in a breeding unit of 2,000 cows:—

(1) 40 young bulls to be tested in each 3-year period;
(2) 1200 cows mated annually to young bulls;
(3) Two proven sires mated annually to 800 cows.

The maximum progress under this scheme is 1.7% per year of the average yield, approximately 25lb. of butter-fat over a 10-year period under New Zealand conditions. In a 10,000 cow unit the maximum rate is increased to over 2%.

One of the prerequisites of the optimum structure is that the young bulls may be selected from any of the 2,000 cows in the unit, the only criterion being their production level. If the selection is limited only to bulls out of cows that happen to be pedigree, the genetic progress will necessarily be slower.

The use of A.I. on a large scale will inevitably reduce the total number of bulls used. In Denmark, for instance, where at present nearly 50% of all cows are artificially inseminated (1), the total number of bulls used has dropped by half (2). Unless the breeding work is strictly controlled, this may lead, because of inbreeding, to an increase in the number of animals homozygous for various lethal genes. After only 10 years of A.I., this has already happened in Denmark, where it is shown that of all Red Danish bulls registered in the years 1945-47, in the provinces of Funen and Zealand, not less than 23.3% are probably heterozygous and 17.8% proved heretozygous for a lethal gene which causes paralysis of the hind legs in new-born calves (13). In the very beginning of the A.I. era (1938) the proved heretozygotes amounted to only 6.6%.

There are two possible methods of avoiding a near calamity of this kind:—

(1) Test-mating all bulls intended for A.I.;
(2) Avoiding inbreeding.

Under the first system, all young bulls under progeny test must, in practice, be mated to at least 20 of their own daughters for their first calf. Because this reduces the number of cows that can be mated with progeny-test sires, the optimum rate of progress will decline from 1.7% to 1.6%.

It is obvious that this method would not succeed under a Sire Survey scheme of progeny test, in that it would not be possible to enforce that commercial breeders test-mate all their bulls on the outside chance that they may be used for A.I. in the future. Neither is the test-mating of sires selected for A.I. feasible, because in most cases a new crop of daughters has to be bred for the purpose, which delays the use of the bull by another three years.

To avoid inbreeding it seems necessary to organise A.I. into a number of isolated breeding units and interchange tested bulls when the risk of inbreeding becomes apparent. This method has the added avantage of maintaining a high degree of genetic variability on which the future progress of a selection programme depends.

It may now be asked for how long genetic progress can be maintained under a selection programme. It can be assumed that under selection pressure the genetic variability, sooner or later, will become exhausted, with the result that progress will be retarded and finally stop altogether. Evidence from small animal breeding experiments indicates, however, that long before this happens other factors interfere to cause a retardation of genetic gains (9) (10). These factors are of two kinds:—

(1) Negative correlation of the selected character with general fitness;

(2) Non-additive gene effects.

The mechanisms responsible for negative correlations may be either that some genes simultaneously affect the desired character in a positive direction and general fitness in a negative direction, or that genes affecting these two traits are very closely linked. If the first mechanism operates, no further progress can ever be hoped for, but if linked genes are involved, progress may recommence after a lag during which time genic blocks of different content may form as a result of crossing over. During the lag phase it is necessary to keep up selection pressure, otherwise a regression towards the starting point may occur.

In some selection programmes the genetic variability may remain relatively high, but if it is mainly due to non-additive gene effects selection gains will become progressively slower.

In view of the fairly weak selection pressure that, up to the present, has been applied to the dairy cattle population in New Zealand, it seems unlikely that a lag phase will be reached for many generations to come.

In the whole of the previous discussion it has been presumed that the sole criterion of selection is the production of butter-fat per cow. In New Zealand emphasis has recently been placed on the production per acre, as a standard of technical efficiency. This in part depends on the efficiency with which the cow converts the feed she eats into butter-fat, which in turn is controlled by two characters known to be inherited: her total butter-fat production and her size. Thus it may be desirable to select for production per cow in relation to her body size rather than for production alone. This refinement in the aim of selection does not, however, invalidate any of the previous conclusions.

The arguments in this paper pertaining to the major influences of environment as a cause of differences between herd averages may suggest that the possible increase in butter-fat production through an overall improvement of feeding and management is so great that the slow and tedious increase that can be effected by better breeding methods will be dwarfed in comparison and therefore hardly worth while. However, despite the ample experimental and statistical evidence that improvement of environment can easily effect a great increase in production, and despite the wide dissemination of this knowledge amongst farmers, there has been hardly any increase in production either per cow or per acre during the last ten years in New Zealand. A likely explanation is that farmers in this country are not prepared or not able to apply any more energy to further improvement of the environment. If this is the case, herd improvement through organised breeding assumes much greater importance, as it does not add materially to the farmers' already overstrained capacity.

TABLE I.

STATION TEST		FIELD TEST		FIELD + A.I.	
Advantages	Disadvantages	Advantages	Disadvantages	Advantages	
a) Highly accurate; as a consequence a minimum number of daughters per bull are required. b) In conjunction with A.I. it is possible that the bulls are mated to a random sample of cows from genetic points of view.	a) Likely to be expensive and as a consequence only a few bulls would be tested. b) Possible genotype interaction cannot be detected as the daughters of each bull are subjected to only one specific environment.	a) Tests are carried out in the course of normal herd testing and are therefore cheap. Many bulls can be tested.	a) Fairly inaccurate as progeny groups are subjected to different environments. Bulls cannot be compared unless correction is made for differences in herd environment. b) Some differences between progeny groups may be due to differences in the genetic value of the bulls' mates. No obvious method for correction for this is available. c) Genotype environment interaction cannot be detected.	a) No correction for environmental differences between bull groups are necessary. b) By mating the bulls to a random sample of cows no part of the difference between progeny groups can be due to differences in the genetic make-up of the bulls' mates. c) By mating the bull to cows of high and low producing herds it is possible to detect genotype-environment interaction.	a) Very inaccurate as large environmental variations within the progeny groups mask the genetic differences between them.

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APPENDIX.

Tables I. and II. summarise the analyses of the published results on the 7th Edition (1949-50 season) of the Sire Survey and Merit Register of the Herd Recording Council, New Zealand Dairy Board.

The data have been analysed separately within each of the three types of survey. The official minimum requirements for the issue of these categores are as follows:—

Final: 10 first, 8 second and 6 third lactations.

Intermediate: 10 first, 8 second lactations.

Preliminary: 10 first lactations.

Since (Table I.) the expectancy formulae differ significantly for the three types of survey, the appreciate formulae are listed in Table II.

y = average butter-fat yield of bull's daughters (corrected to mature equivalent) (lb.).

x = average yield of mature cows in testing herd (lb.).

TABLE I.—Regression Analysis.

Type of Survey	Sums of squares and products				S.S. due to regression (1 d.f.)	Residual	
	d.f.	(y2)	(xy)	(x2)		d.f.	s.s.
Preliminary	451	934,955	725,485	926,823	567,585	450	367,070
Intermediate	348	666,493	486,058	569,681	414,710	347	251,783
Final	568	1,131,833	950,890	1,082,177	835,530	567	296,303
						1,364	915,161
Total	1,367	2,733,281	2,162,433	2,578,681	1,813,375	1,366	919,906
Difference (variation in regressions)						2	4,745*

* Significant at 5% level.

TABLE II.—Summary and "Expectancy" Formulae.

Type of Survey	Total bulls	Mean daughter average (x)	Mean mature cow average (x)	"Expectancy equation" (Y = expected daughter average)	Standard (from deviation regression)	Percentage variation due to regression
Preliminary	452	318	322	Y = .783x + 65.3	28.6	61%
Intermediate	349	318	321	Y = .853x + 44.2	26.9	62%
Final	569	324	327	Y = .879x + 36.8	22.9	74%

NOTE: (1) Analysis based on **unweighted** averages (ignoring number of records per bull).
(2) Figures shown refer to deviations from survey means.

Discussion

Miss CASTLE: Mr. Hancock stated that he had calculated his "Expectancy" value from results of surveys published in the 7th edition of the Sire Survey and Merit Register. It is essential that "Expectancy' values be based on a random sample of bulls in each productiton level. With herds under Group Test we are able to satisfy this condition as surveys are issued automatically as soon as there are sufficient daughters of the bull under test. However, owners have the right to refuse publication of Preliminary and Intermediate surveys so that the results published in the Register do not represent a random sample of bulls. They also include some surveys for bulls in herds not under Group Test. These had been issued on application by the owner and again could not be said to constitute a random sample as they were all in the higher ranges of production and all above "Expectancy." Inclusion of these survey results would tend, therefore, to make the regression line steeper.

If our regression line were not steep enough this would mean that we were being somewhat lenient with bulls used in high-producing herds. As we have evidence that bulls used in these herds are of better quality than those used in low-producing herds we would not be unduly worried by this, as we are measuring them against a better than average sample of bulls in any case. Again even if the slope of the regression line were .85 instead of .75 this would not markedly affect the values for the majority of surveys which, of course, lie in the central ranges of production.

One would expect the regression line for Final surveys to be steeper than the line for Preliminary surveys as most Final surveys are based on four or five seasons' records whereas the majority of Preliminary surveys would include only one or two seasons' records. As the repeatibility of a mature cow average based on one season only would not be as high as one based on several seasons, there would be a greater regression to the mean in the case of Preliminary surveys.

Our "Expectancy" values are reviewed and if necessary amended when each season's surveys have been completed.